

A NEW MIDDLE EOCENE SHOREBIRD (AVES: CHARADRIIFORMES, CHARADRII) WITH COLUMBOID FEATURES

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ABSTRACT: *Plumumida lutetialis* new genus and species is the third fossil bird to be described from the Messel site in West Germany. It is based upon a fractured postcranial skeleton and is referred to the Charadrii on the basis of numerous skeletal features. It deviates from all living and known fossil shorebirds by having a strong perching foot and skeletal structures in the pelvis and hindlimb considered to be connected with such specialization. By the form and supposed function of the foot the fossil bird shows similarity to the doves, but other dove apomorphies are lacking. Two skeletal features that may be autapomorphies for the group to which *Plumumida* belongs set the bird apart from the doves. *Plumumida* is believed to be related to those early shorebirds that are thought to have given rise to, among others, the doves; the genus is placed *incertae sedis* in the Charadrii. The depositional environment of the fossil is reviewed.

ZUSAMMENFASSUNG: Ein neuer Stelzvogel, *Plumumida lutetialis* gen. et sp. nov., wird als dritter fossiler Vogel aus dem Messeler Ölschiefer beschrieben. Die Art gründet sich auf ein postkraniales Skelett, das mässig verdrückt und unvollständig ist. Die osteologischen Merkmale deuten auf eine Verwandtschaft mit den Charadrii hin. Der Vogel unterscheidet sich jedoch von allen heutigen und fossilen Charadrii durch einen Sitzfuß. Zu einer solchen Spezialisierung passen auch die gefundenen Skelettstrukturen im Bein und Becken. In Form und mutmaßlicher Funktion des Fußes ähnelt *Plumumida* den Tauben, doch sind keine anderen Columbiformen Apomorphien am Fossil nachweisbar. Zwei Skelettmerkmale, die Autapomorphien der taxonomischen Gruppe sein könnten, zu der *Plumumida* eigentlich gehört, unterscheiden den fossilen Vogel von den Columbiformen. *Plumumida* ist zu den frühen (jungkretazisch-alttertiären) Stelzvögeln zu rechnen, aus welchen auch andere Formen, wie allem Anschein nach die Tauben, abgeleitet werden können. *Plumumida lutetialis* wird *incertae sedis* den Charadrii eingegliedert. Ein Überblick über die Lebens- und Einbettungsumstände des Fossils wird gegeben.

Two birds have previously been recorded from the Lutetian (Middle Eocene) deposits at Messel in the West German Bundesstaat Hessen. They are the alleged shorebird *Rhynchaëtes messelensis* Wittich 1898, and *Diatryma* cf. *steini* Matthew and Granger 1917 (Berg 1965). The purpose of this paper is to describe a new shorebird from the Messel oilshale that is about the size of *Rhynchaëtes messelensis*, but differs from that form in skeletal morphology and relative proportions, and from living shorebirds by having a perching foot.

The Messel site has yielded large quantities of fossil animal and plant remains, many of which have only recently been discovered. The total number of bird fossils so far secured from the site comes to over one hundred. Among these, more than fifty were kept by Frau E. Soergel in Freiburg im Breisgau (Tobien 1969:165), but these have now been returned to the Hessisches Landesmuseum in Darmstadt, West Germany, and about forty are under investigation by Dr. D.S. Peters at

the Forschungsinstitut Senckenberg, Frankfurt am Main, West Germany. Such abundance, and the tragic fate now threatening the Messel pit from local authorities in one of industrial Europe's most densely populated areas, justifies a brief introductory description of the site.

THE MESSEL SITE

The Messel pit is located about 9 km NE of Darmstadt and 22 km S of Frankfurt am Main. It now appears as a 1000 by 700 m crater, 60 to 70 m deep, the bottom of which became covered by a shallow lake after mining was stopped in 1971 (Fig. 1). The pit was formerly exploited for oilshale, and produced about 1 million tons of crude oil used as fuel and for the manufacture of various products for the dyestuffs, electronics, chemical, and pharmaceutical industries until the site was closed down.

The oilshale was discovered in the mid-1870's, and exploitation began in 1886. The shale deposit is known to have had a maximum thickness of 190 m in the Messel pit, and there are other, smaller oilshale pits in the area. The shale occurred

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Figure 1. The Messel site at the end of February 1978. Photograph by J.L. Franzen (Senckenberg Museum, Nos. 296–297).

below Middle Eocene strata containing brown coal lenses up to 2 m thick (Franzen 1976a). Through the years 1886–1971, many specimens of fossil leaves, wood, insects, fish, frogs, tortoises, lizards, snakes, crocodiles, birds, and mammals were found and recovered by those working in the open air Messel pit (Tobien 1957), and by the Darmstadt Museum. Fossils were also obtained from the nearby Prinz von Hessen oilshale pit in the years 1912–24 (Franzen 1978). Unfortunately, because of the large water content (up to 40 percent) and the chemical constituents of the shale (marcasite in particular), combined with the state of knowledge of preservation techniques at that time, many of these fossils are now in a most miserable condition.

With the introduction of the “cast resin transfer method” (see Bornhardt 1975) developed in England in the 1950’s (Toombs and Rixon 1950; see also Rixon 1976) and first applied to the Messel fossils by Dr. Walter Kühne in the early 1960’s (Kühne 1961, 1962), a new period of preservation of the oilshale specimens began. The resin impregnates and locks the bones of one level of the fossils, thus hardening and supporting them sufficiently for further manipulation and studies, as well as for exhibition purposes. However, the parts of the fossil specimens that are not impregnated by the resin, or that do not adhere to it, are often lost.

A veritable fossil-rush followed the closing of the mine works in 1971. A multitude of collectors, most of them laymen, searched for traces of ancient life in the pit, not always to the good of the desired objects. Authorities finally had to take steps to safeguard, not so much the site, but the lives of the fossil hunters. At the end of 1974 the admittance of non-authorized persons to the site was prohibited.

Permission to collect fossils in the Messel pit was granted to the Hessisches Landesmuseum Darmstadt in 1913. This institution was the sole authorized collector until 1975 when the Forschungsinstitut Senckenberg, the University of Hamburg, and the Museum für Naturkunde Dortmund also obtained the right to conduct scientific investigations of the site. A large project is now in progress, financially supported by the foundation “Volkswagenwerk,” involving many scientists and good amateurs working under the leadership of Dr. Jens Lorenz Franzen, Forschungsinstitut Senckenberg (Franzen 1978,

1979). More than 18,000 fossils have been recovered to date, the most conspicuous fossil group being perhaps the perissodactyls, *Propalaeotherium* spp. (first thoroughly described by Haupt 1925), although the holosteans *Amia* and *Atractosteus* (Lepisosteidae) and the salmoniform *Thaumaturus* are the most numerous vertebrates. Among the tetrapods, birds and bats dominate (Franzen 1979). A list of fossils is given by Koenigswald (1979). Several forms hint at a NW Europe–North American land connection that persisted until about the end of the Early Eocene (West et al. 1977; Berggren et al. 1978).

The fossils of the Messel oilshale are often, except for a certain flattening, exceedingly well preserved when found. Not only do major parts of bony skeletons occur, generally in articulation, but in many cases the specimens show substantial “shadows” of the organisms’ soft tissues. Hair, feathers, and traces of colors in chitinous insect parts may occur at the site (Haupt 1925; Franzen 1976b, 1979). Even the cuticular structures of partly digested leaves in the intestines of some fossil herbivores can be studied in detail. For example, there have been investigations into the stomach contents of *Propalaeotherium messelense* (Franzen 1976b, Sturm 1978). These studies have, in turn, given material support to the hypothesis (first advanced by Kowalevsky 1873–1874; see also Strelnikov and Hecker 1968) of a habitat and food change during the evolution of horses (*sensu lato*) from pre-Miocene softground forests to grass plains, and from “omnivorous” to purely graminivorous equids, respectively.

Presented against this background, recent proposals for the future of the Messel pit evoke the quotation of a heading in the catalogue for the Senckenberg Museum Messel exhibition (Franzen 1977:24): “Wen interessiert eigentlich der Mageninhalt des Urpferdchens?”—“To whom is the stomach content of the protohorse of any real interest?” There are very few sites in the world where remains of an Eocene continental flora and fauna occur in such abundance and good state of preservation as at Messel. These fossils permit a multitude of scientific investigations and conclusions concerning evolution and the ecological, climatological, and physico-chemical aspects of the paleoenvironment. But, instead of preserving the Messel site and its fossils for the progress of knowledge, there are now official plans for the Frankfurt-Darmstadt-Dieburg-Offenbach

metropolitan area to use the Messel pit for a large scale garbage disposal! This would also include so-called "non-dangerous industrial waste products." It may be true that large refuse accumulations are an inevitable result of modern environmental policy, but it is questionable if it is really necessary to install a giant garbage dump exactly in the Messel pit! Such short-sighted solutions to man-made problems are highly tragic, especially when viewed against the history of life.

AGE AND ORIGIN OF THE MESSEL OILSHALE

Judged from its fossil content, the bituminous deposit is of Lutetian age, 43 to 49 million years ago (Berggren 1972, and following the time scale agreed upon by workers presently studying the Eocene North Sea tetrapods in the "Projet 124 du Programme international des corrélations géologiques"). Tobien (1968, 1969:169) refers the oilshale to early Lutetian age on the basis of contained mammals. This is questioned by Franzen (1976a:422), however.

During middle to late Eocene times, Tertiary Europe experienced its maxima of temperature and marine transgression. Surrounded by the Atlantic Ocean, the North Sea, and the Tethys Sea, the two latter being connected over present-day Poland (Russell 1975; Bond 1978; Heissig 1979), the "Mid-European land" had a humid subtropical-tropical climate (Němejc 1970; Buchardt 1978), as is also indicated by the rich bitumen and lignite deposits formed at that time.

The Lutetian Messel lake and neighboring lakes developed concurrently with tectonic rifting of the area, as part of a larger river system (Tobien 1969). Detailed investigations, in particular of the location and orientation of fish fossils *in situ* in the oilshale, reveal the influx of two main water currents in the Messel lake, one from the northeast and another from the northwest, and the outflow of a current at the southern edge of the lake (Franzen 1979). Related studies (*ibid.*) have also shed light upon the distribution and probable local geographic derivation of the fossil organisms in the oilshale. The Messel flora and fauna were part of a warm, damp Eocene jungle environment. In its rivers and lakes the near-surface life was abundant, but the deep bottom waters were quiet and dark with anaerobic conditions. Thin strata of mineral particles and organic debris accumulated, embedding those parts of larger carcasses that were not devoured on their way down through the waters.

Towards the end of the Middle Eocene the lakes developed into swamps that were invaded by land plants. These plants gave rise to the lenses of brown coal that overlie the oilshale.

OTHER SITES IN WESTERN EUROPE WITH EOCENE BIRD REMAINS

European geography was subjected to great changes during Paleogene times. The interrelated Alpine folding and Rhine-graben rifting determined the formation of the central European tectonic features (Illies 1978; Illies and Greiner 1978), including the primary Messel lake. And North Atlantic rifting continued the rupture of the northern landbridge between Europe and North America. *Diatryma* occurred at Messel (Berg 1965), Geiseltal (Fischer 1967, 1978), and in France (Gaillard 1936) during the Middle Eocene, and is recorded from Upper

Paleocene and Lower Eocene beds in north America and France (see Brodkorb 1967).

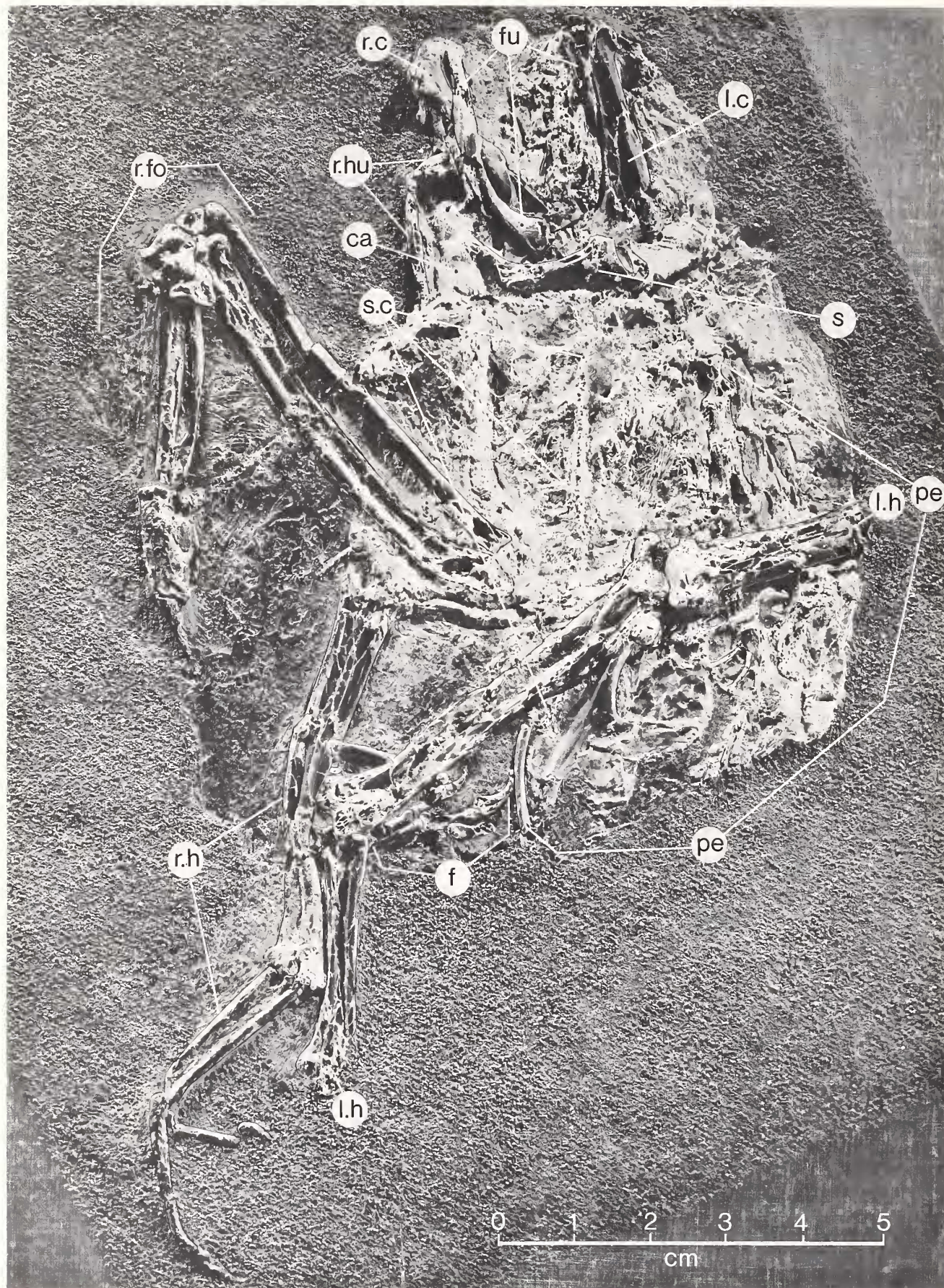
Briefly mentioned below are some Eocene sites in western Europe of interest to paleornithologists; faunistic or chronologic intercorrelations have not been made, nor have correlations with Eocene sites outside western Europe. Relevant literature older than that referred to can be found in the cited works.

British deposits yielding Eocene birds are known from the southeastern part of England; these fossils have most recently been discussed by Harrison (1971), and Harrison and Walker (1977). In France, Eocene bird remains are recorded from the Paris basin (Louis 1969; Brunet 1970; Hoch 1975); the bone-fissures of Quercy, or "les Phosphorites de Quercy" (Gaillard 1939; Collins 1976; Mourer-Chauviré this vol.); the Lower Eocene egg-bearing beds of Provence that are part of an upper Cretaceous-lower Tertiary series containing bones and eggshells of dinosaurs and eggshells of large birds (Touraine 1960, 1961; Dughi and Sirugue 1962); the Lutetian Strait of Carcassonne sediments with bird tracks (Plaziat 1964); and the sites that produced *Diatryma* referred to above. From Switzerland are known the Egerkingen siderolithic bone-fissures (Schaub 1940). A reputed bird-yielding locality in East Germany is Geiseltal, where fossils are occasionally even better preserved than in Messel (Lambrecht 1935; Fischer 1962). Fissure-fillings in the Schwäbischen and Fränkischen Alb in southern West Germany also contain bird bones (Dehm 1935). Within the Eocene North Sea area, fossil birds occur, outside England, at various sites in Denmark and northern Germany (Hoch 1975; the lower Mo-clay and Clay with Tuff deposits with bird fossils are now assigned to the Upper Paleocene, Hansen 1979).

GENERAL REMARKS ON THE FOSSIL BIRD AND ITS CLASSIFICATION

The specimen considered here (Fig. 2) is an incomplete, partially articulated skeleton of a small to medium size bird. It is flattened in an oblique, dorsoventral direction, and is shown from the ventral side in Figure 2. The dorsal side, the one exposed when the fossil was excavated, is now embedded in an artificial matrix (plast resin).

The right fore- and hindlimbs (Fig. 2, r.hu, r.fo, r.h) are turned out and rest beside the body. The left hindlimb (l.h) crosses over the abdominal area to lie alongside the right hindlimb. Soft tissue evidently still remained when the carcass was embedded in the lake sediments, and it determined the almost natural position of the limb bones relative to the body. The toe complex of the left foot (f) apparently became displaced not too long after deposition, and is now located around the distal end of the left tibiotarsus. No skull is preserved, which seems to be fairly usual for bird fossils from the Messel site (Franzen 1978:126). Other skeletal elements lacking or being unidentifiable in the fossil include most of the pre- and post-synsacral sections of the vertebral column, the ribs, the entire left forelimb, and two toes of the right foot. Generally speaking, the bones are fragmented and more or less incomplete, and their ends, in particular, are poorly preserved. In some places molds made of the embedding resin render the missing bone parts in indistinct contours. The state of preservation of the fossil seems similar to that described by Russell and Sigé (1970) for bats from the same locality.



In spite of its incompleteness, sufficient morphologic skeletal characters can be observed in the fossil for an allocation of the bird to taxonomic order. The concept presented by Bock (1974:383) at a symposium on contemporary systematic philosophies in 1973, advocating the presentation of the classification in the introduction instead of at the end of taxonomic papers, will be followed here: "... the reader [then] knows what statements are available for disproof, what tests will be attempted and hence why certain empirical evidence is being presented."

After comparison with relevant Recent and fossil birds, the specimen is referred to the Charadriiformes, and to the sub-order Charadrii therein. Decisive for this taxonomic allocation is a suite of observable characters, which may or may not be unique for the Charadrii, but which taken together occur only within the group of birds traditionally regarded as shorebirds. I am here following Strauch (1978:270) when he states, referring to works by D.H. Colless, that one is forced to start with some sort of phenetic estimate of relationship as a beginning of a phylogenetic study. The fossil's state of preservation does not permit sophisticated morphologic deductions. Rather, it seems that the present paleontological work is one of those where, as pointed out by Cracraft (1972a:384), the use of overall resemblance is inevitable.

The fossil bird is considered to be related to those early Cenozoic "lapwings" and "coursors" that, according to Fjelds  (1976, pers. comm.), were specializing towards the sandgrouse/dove complex. In these "basal waders," the hindtoe had not been reduced and specialized to a cursorial life, as is the case in modern shorebirds. The Lutetian bird can be characterized as a robust member of the Charadrii with specializations simulating the doves: "a perching shorebird."

Features that refer the fossil to the Charadrii are:

1. A U-shaped furcula with a sturdy symphyseal part (Fig. 2, fu; Fig. 3, fu). In general morphology this latter part resembles those depicted by Strauch (1978: Fig. 22b, c) as typical of shorebirds. In doves, the furcula is weak.

2. A long sternal plate (Fig. 2, from s along the length of s.c), a good-sized carina with a distinctive pillar-like strengthening of the anterior edge (Fig. 2, ca, s.c; Fig. 3, ca, a.c), and the morphology of the anterior articular area. In ventral view the sternum shows, as exposed in the fossil, a fragmented strong anterior medial "lip" (Fig. 3, v.m), believed to be the base of a large ventral manubrial spine that overhangs the coracoidal sulcus (Fig. 3, c.s). The observable part of the sulcus for the left coracoid suggests a structure that was unbarred in lateroventral direction, and had a voluminous dorsal lip (see Description), both features also in harmony with shorebird morphology. No trace of a dorsal manubrial spine can be distinguished in the fossil, most probably because it was never there, which would agree with conditions in the Charadrii. In doves there are both ventral and dorsal manubrial spines, and the ventral one is small and does not "overhang" the coracoidal sulcus.

3. The relative proportions and the morphology of the wing bones (Fig. 2, r.hu, r.fo), in particular those of the hand. Part of the proximal end of the right humerus (Fig. 3, h.h, e.t, d.c) is preserved in the fossil. In the right elbow joint area (as determined by the position of the ulna and radius), there are crushed bone material and contours that are difficult to distinguish in the figures; these in all probability indicate the location of the distal end of the humerus. This will permit the statement that the ulna-radius segment is the longest of the forelimbs, with the humerus and hand segments about equally long and somewhat shorter than the ulna and radius (see Measurements below). Similar relative forelimb proportions are encountered in a large number of bird taxa, but other taxa differ from the common pattern, e.g., rails, where the humerus is longer, and doves, where the hand is longer. In doves the humerus is noticeably large and "swollen," but it is by far the shorter of the three mentioned segments. In the fossil, those traces of the humerus that are preserved testify to a fairly "ordinary" shape and to proportions corresponding to humeri in shorebirds (see Description). The carpometacarpus (Fig. 4, cm), by its long distal symphysis of metacarpals II and III, its fairly straight metacarpal III, and other morphologic features, suggests relationship with the Charadriiformes as well as with the Anseriformes. The strong basal part of metacarpal I (unfortunately its process is not preserved in the fossil), as pointed out to me by Jon Fjelds , could very well indicate that this part of the carpometacarpus had a spur-like process as is found in, among others, many lapwings, and, as a potential preadaptation, throughout the plovers and allied groups. Such a character might not, however, exclude the Anseriformes from consideration, among which *Anseranas* has spurs on metacarpal I. The character may be primitive within the shorebirds, ducks, and a few other groups, corresponding to their supposed phyletic relationship and derivation from a common stock (Fjelds  pers. comm.). The observable morphology of the proximal phalanx of digit II (Fig. 4, d.II) corresponds to that in shorebirds such as *Vanellus* and *Pluvialis*. The element is believed to have been unfenestrated (a small hole (x) in the preserved lamellar bone in the fossil is a fracture), a state that excludes the bird from the Lari (Lydekker 1891), and in part the Glareolidae, within the Charadriiformes. There is general agreement that a non-fenestrated proximal phalanx of the hand-digit II (Strauch 1978:314: "digit III" error for digit II) is primitive in the Charadriiformes. The same element in doves shows a certain morphologic similarity to that in shorebirds but seems more "elaborated," with, e.g., the internus indicis process (corresponding to p, Fig. 4) much stronger than in unspecialized shorebirds, as is also indicated by Stegmann (1969:10 and Fig. 8). In doves the bone is also non-fenestrated.

The coracoids, pelvis, and long bones of the hindlimbs are reminiscent of those in shorebirds, but may at first sight be ascribed some dove traits. The coracoids (Fig. 2, l.c, r.c) are fairly long and straight with a short external lip of the glenoid facet (Fig. 3, g.l). Both in relative proportions and in detailed

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Figure 2. *Plumumida lutetialis* new genus and species. Holotype. Middle Eocene oilshale at Messel, Hessen, West Germany. S.G.P.I. Kat. Nr. 2183, Hamburger Geologisches Institut (Section of Palaeontology). The specimen is mounted on a slab of plast resin with a thin sediment coating. ca, sternal carina; f, toe complex left foot; fu, furcula; l.c, left coracoid; l.h, left hindlimb; pe, pelvis; r.c, right coracoid; r.fo, right forelimb, sub-elbow part; r.h, right hindlimb; r.hu, right humerus; s, sternum: anterior end; s.c, sternum: broken base of the sternal carina.

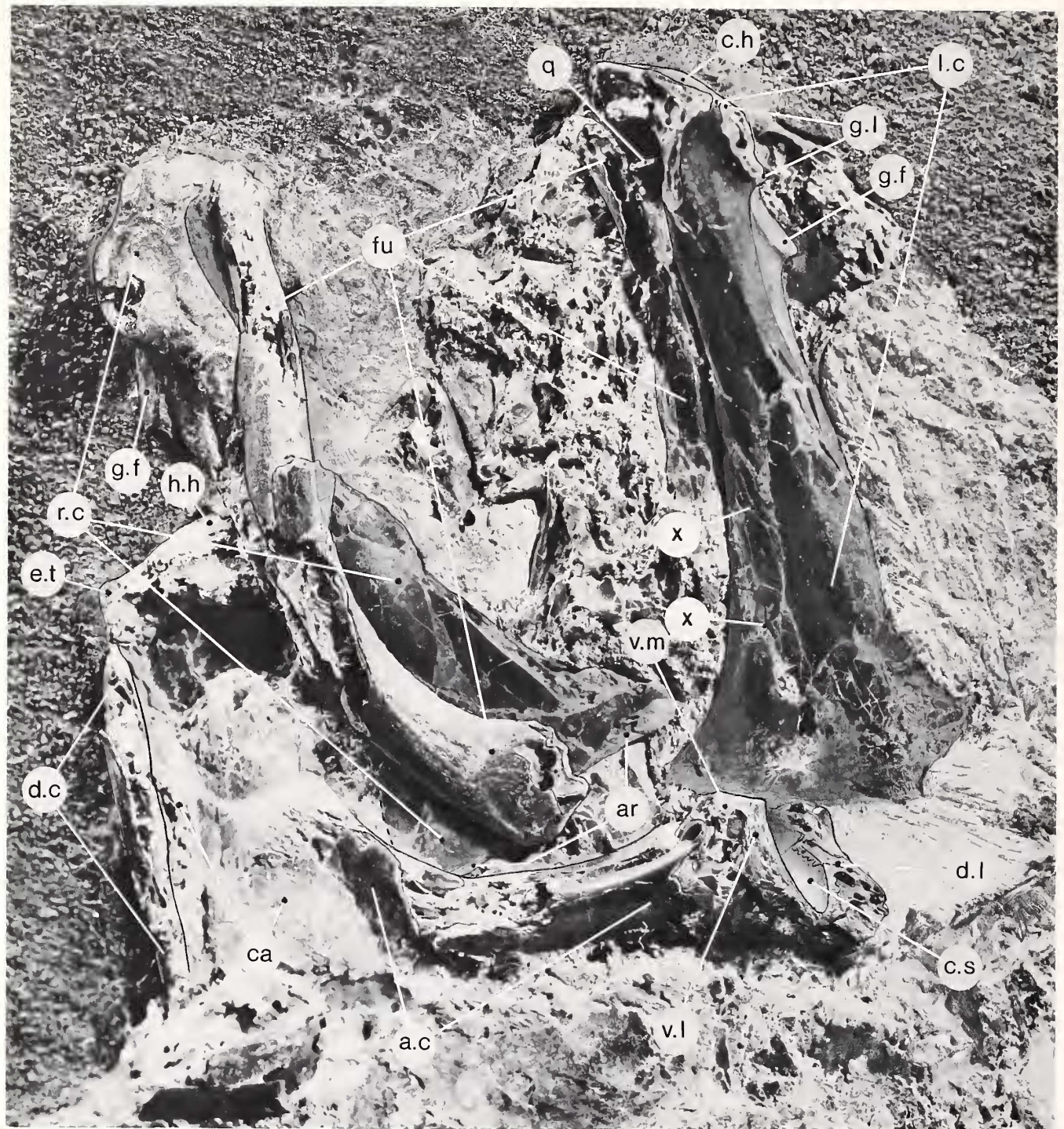
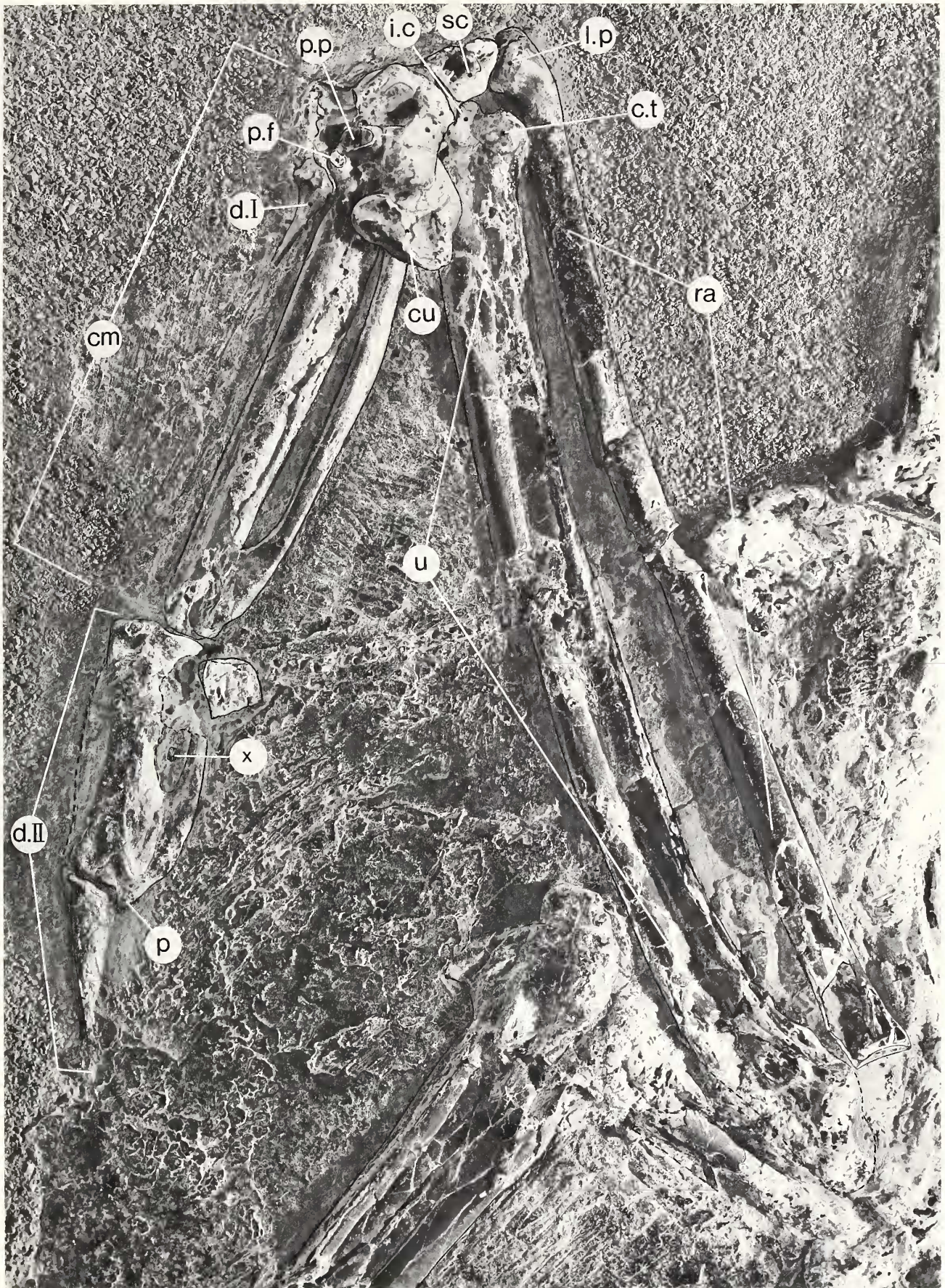


Figure 3. Shoulder girdle of the holotype of *Plumumida lutetialis*. a.c, anterior carinal margin of sternum; ar, articular markings at sternal edge of coracoid; ca, sternal carina; c.h, coracohumeral surface; c.s, coracoidal sulcus; d.c, deltoid crest of right humerus; d.l, dorsal lip of coracoidal sulcus; e.t, external tuberosity of right humerus; fu, furcula; g.f, glenoid facet; g.l, glenoid lip; h.h, humeral head; l.c, left coracoid; q, ?procoracoid; r.c, right coracoid; v.l, ventral lip of coracoidal sulcus; v.m, base of ventral manubrial spine; x-x, natural depression in coracoidal bone wall.

Figure 4. Right forelimb of the holotype of *Plumumida lutetialis*. cm, carpometacarpus; c.t, carpal tuberosity; cu, cuneiform; d.I, digit I; d.II, digit II; i.c, internal condyle; l.p, ligamental prominence; p, internus indicis process; p.f, process pertaining to pollical facet; p.p, pisiform process; ra, radius; sc, scapholunar; u, ulna; x, fracture in lamellar part of proximal phalanx of digit II.



morphology, as far as they can be discerned in the fossil, they are closer to those in shorebirds, e.g., *Charadrius*, than to those of doves (see Description). The pelvis (Fig. 2, pe) is a robust, short and wide element with distinct and fairly large iliac and ischiatic posterior processes. The robustness of the pelvis corresponds to that of the bones of the fossil in general. Robustness characterizes the pelvis, as well as the entire skeleton, of many doves, but such shorebirds as the oystercatchers, which some authors (e.g., Fjelds  pers. comm.) regard as primitive among Recent Charadrii, also have fairly robust skeletons. The visual impression of wideness of the fossil pelvis is exaggerated because of the flattened condition of the specimen. The shape of the posterior pelvic processes are, in fact, dove-like, as are some other details of the pelvis. The hindlimbs are dove-like, although some fine morphological features in the long hindlimb bones are shorebird-like. The relative proportions of the bones and the shape of the foot show similarity to the condition in doves.

The taxonomic status of the fossil at the family level has been subject to considerable circumstantial consideration. Judged from observed characters the bird does not fit into any of the generally acknowledged shorebird or dove families, and no living birds are found that exhibit intermediate shorebird-dove morphology (Stegmann 1969). Some paleontologists prefer the erection of a separate family for such a form, in order to (1) indicate that the bird is an aberrant but valid member of the order and suborder to which it is referred, and (2) secure it from being consigned to oblivion by being placed *incertae sedis* somewhere in the system when future reorganizers of the avian hierarchy find it a burdensome misfit. Another point of view is that such a monotypic bird family, based upon a single incomplete fossil exhibiting aberrant features, will be a nuisance to anyone who wants to make practical use of the bird system, and consequently that the bird should be included in one of the existing families.

According to Fjelds  (1976, pers. comm.) the early shorebirds, from which a cursor/sandgrouse/dove line can be derived, constituted the basic charadriiform group, together with the stone curlews that are close to the lapwings (compare Cra-craft 1972b). Fjelds  groups some Recent Old World species (generally regarded as lapwings), which "must be very close to the basal late Cretaceous wader stock," in the genus *Xiphidiopterus*, while even the living stone curlews, oystercatchers, avocets, and certain others are "basal" in several aspects, although each group has its own specializations. Fjelds 's system is based on studies of Recent birds. It seems unjustifiable, on the basis of present evidence, to refer the Lutetian bird to any of Fjelds 's charadriiform taxa. The bird, by the structure of its foot, is evidently different from known shorebirds and their allies, the foot resembling that of doves. But a number of clearly apomorphic traits of doves (and sandgrouse and cursors) are missing. Reduction of the hindtoe is apparently habitually conditioned in plovers and other shorebirds: it tends to disappear in cursorial inhabitants of arid plains, whereas a small hindtoe remains in inhabitants of marshy environments (Fjelds  1976). A well-developed hindtoe is considered a plesiomorphic character within the Charadriiformes, in accordance with Strauch's view (1978:320). The strong development of the hindtoe in the Lutetian bird, as part of a perching foot type, may be a plesiomorphic state. But rather, the whole foot structure should be regarded a specialization, paralleling that

in doves, that sets the fossil bird apart from the Charadriidae *sensu* Fjelds  (including oystercatchers, stilts, and avocets). The fossil bird will be placed *incertae sedis* in the suborder Charadrii, a provisional status open to reconsideration when further evidence becomes available through new finds of fossil material. There are good possibilities for this, if paleontological work can be continued at the Messel site.

SYSTEMATICS

Order Charadriiformes

Suborder Charadrii—Shorebirds

Family *incertae sedis*

Plumumida new genus

TYPE SPECIES: *Plumumida lutetialis* new species.

INCLUDED SPECIES: Type species only.

DIAGNOSIS: Shorebirds with a robust skeleton, the forelimbs longer than the hindlimbs. The coracoid has a long and distinct glenoid facet with a glenoid lip that is short in basal extension. The carpometacarpus has a distal metacarpal symphysis that is about one-fifth its length. The pelvis and hindlimbs show features reminiscent of doves. The synsacrum has the anterior part of the caudal section broad and flat ventrally, with two pairs of ventral parapophyses. The foot is a strong perching foot.

DISTRIBUTION: So far confined to the Middle Eocene (Lutetian) of Germany (BRD).

ETYMOLOGY: Latin, *pluma*, feather; and Latin, (*h*)*umida*, moist. The name alludes to the only true story we know of the bird, i.e., that it was post-mortem soaked in the Eocene Messel waters. The sound of the name may invoke the impression of the plumpness that characterizes the fossil bird skeleton, but it also conveys the feeling of the deep, dark mud that softly veiled the dead bird on the lake bottom and held it for over 40 million years.

Plumumida lutetialis new species

HOLOTYPE: An incomplete, articulated, obliquely dorsoventrally flattened and partially crushed skeleton now preserved on a slab of artificial resin. Hamburger Geologischen Institut (Section of Paleontology), S.G.P.I. Kat. Nr. 2183; collected by Mr. Hans-Peter Schi rning, Hamburg, West Germany, in 1972.

TYPE LOCALITY: The Messel oilshale pit, West Germany. According to the finder (letter of 24 November 1978): "Die Fundstelle liegt am westlichen Hang der Grube Messel auf der vierten Sohle des fr heren Tagebaus. Die Schichten sind nicht bestimmbar, da eine Festlegung wegen fehlender Merkmale bisher nicht erfolgen konnte. Alle Ablagerungen fallen stark nach Osten ein."—"The fossil was found on the western slope of the Messel pit at the fourth exploitation level of the ancient open mine. The layers [with the fossil bird] cannot be correlated with others in the pit because stratigraphic indicators are lacking. All strata dip strongly towards the east."

DIAGNOSIS. As for genus.

ETYMOLOGY: Latin, *Lutetia*, Paris (that gave name to the Middle Eocene stage, the Lutetian, of western Europe);

and Latin, *-alis*, belonging to. In reference to the time when the bird lived.

MEASUREMENTS (in mm): Since all bones measured in the fossil are in some state of fragmentation and/or incompleteness, the measurements given are approximate. Shoulder girdle and forelimb: coracoid (shortest distance from top of bone to edge with sternal facet) 30; humerus (from top of head to elbow joint as determined by the proximal ends of ulna and radius) 58; ulna (maximum extension) 61; radius (maximum extension) 59; carpometacarpus (maximum extension) 34; phalanx 1 in digit II (length between metacarpal and digital facets) 15; total hand (from top of carpometacarpus to end of digit II) 58. Hindlimb: femur (see Description) 36; tibiotarsus (from proximal articular surface to, and including, distal condyles) 56; tarsometatarsus (maximum extension) 36; phalanx 1 in digit I 9.

DESCRIPTION: The bone terminology used is primarily that of Howard (1929).

The Shoulder Girdle. In this section of the holotype (Fig. 3), the furcula (fu) is seen displaced a little toward the right side of the bird relative to the coracoids, so that the right and median parts of the furcula are now resting on top of the right coracoid (r.c). The left furcular branch is located alongside the medial edge of the left coracoid (l.c). In the symphyseal region lies the anterior and stronger part of the sternum, turned out of its original position and partly crushed. The thickened anterior carinal margin (a.c) occupies a more or less transverse position in the figure, corresponding to an overturning of the carina toward the right side in the fossil. The left coracoidal sulcus (c.s) is exposed and can be followed into the matrix above the anterior part of the ventral lip (v.l). Medial to the latter is the broken base of the ventral manubrial spine (v.m), as referred to above. The remains of the left dorsal lip (d.l) show that this structure attained its largest size toward the lateral termination of the coracoidal sulcus. The anteroventral termination of the carina is difficult to determine. Lamellar bone now adhering to the inner side of the deltoid crest (d.c) of the right humerus and covering the area between this and the anterior carinal margin is believed to belong to the carina (ca). Its natural edge is not preserved. Most of the carinal base (Fig. 2, s.c), including its triangular xiphial part (Fig. 2, lower s.c; Fig. 6, s.c), can be seen. Lamellar bone alongside the carinal base is either parts of the sternal plate or, as may be the case along its right side, remains of the overturned carina.

The coracoids are strong elements. Compared with coracoids in Recent shorebirds they seem little specialized in their sternal ends, where they show a similarity to the coracoids of such forms as *Haematopus*, *Pluvialis* and *Charadrius*. As seen in ventral view, their broader sternal part (not naturally delimited in the fossil in its present state of preservation) appears to have been moderately rounded from side to side, with a stronger rounding toward the medial edge of the bone. This is visible on the left coracoid, whereas the right one has suffered flattening in this area. The articular markings (Fig. 3, ar), visible in the right coracoid, are relatively small and almost identical in shape with those in *Haematopus ostralegus*. Toward the middle of the shaft, as seen in the left coracoid (Fig. 3, x-x), is a natural depression, also a morphologic correspondence with *Haematopus ostralegus*. An intermuscular line extends along the length of the bone (distinct in the left coracoid, Figs. 2 and 3). The humeral end of the left coracoid

is comparatively well preserved, whereas in the right coracoid the humeral end is mainly in replica and shows no fine morphologic details of the original bone. In the left coracoid the glenoid lip (Fig. 3, g.l), of which only the base remains, is short in basal extension, and the neck of the bone, which is broken, diverges from the mainstem of the coracoid very close to its upper termination. The coracohumeral surface (c.h, only partially visible in the figure) is broad. The shortness of these structures is in contrast to the remarkably long glenoid facet (g.f) sharply set off from the surrounding bone wall. Bordering it sternally is a distinct, oblong-triangular sidewall of the coracoid. The structure indicated "q" in Figure 3 may be the distal part of the procoracoid.

The U-shaped furcula is very stout, or robust, judging from the preserved right side of its middle part and the remains of its branches. A ridge can be followed on the exposed surface of the bone, extending to the lower part of the symphyseal area. The ridge from right and left sides delimits a shallow symphyseal depression in the anterior wall of the furcula. No distinct furcular process can be observed.

The Forelimb. Part of the proximal end of the right humerus can be discerned (Fig. 2, r.hu; Fig. 3, h.h, e.t, d.c). And of the sub-elbow section (Fig. 2, r.fo; Fig. 4), the radius (Fig. 4, ra), ulna (u), cuneiform (cu), scapholunar (sc), carpometacarpus (cm), and digit I (d.I) and digit II (d.II) are comparatively well preserved. No trace is left of digit III.

The proximal end of the humerus is represented by the incomplete head (Fig. 3, h.h), external tuberosity (e.t), and deltoid crest (d.c). The external tuberosity is protruding, forming a "corner" or "shoulder" of the bone; in this character, the bone is similar to the humeri in shorebirds, but differs from those in doves. The base of the deltoid crest, as preserved in the fossil, appears broad and strong. It is fractured and apparently artificially widened, thus seeming broader than it originally was. It is about the same relative length as the deltoid crest in shorebirds. Possible crushed remains and vague imprints of the distal end of the humerus in the elbow area have been mentioned above. No bone fragments or structures in the area between the proximal and the presumed distal end of the humerus can be reliably referred to that bone.

The radius (Fig. 4, ra) and ulna (u) are fairly complete in outline, although their bone walls are fragmented and, especially in the radius, partially in replica. A fracture zone cuts across the middle of the radius and ulna, and disturbs the impression of the form of the bones. The radius was an almost straight bone with a swollen ligamental prominence (l.p). The ulna is crushed in its proximal end, where its limits can be traced against the background only with difficulty. In the distal end of the ulna, the carpal tuberosity (c.t) and internal condyle (i.c) are visible. The carpal tuberosity is a bulging structure with a large terminal ligamental attachment. The fossil ulna exhibits no papillar markings. The anconal papillae, if present, will be situated beneath the plast matrix.

The two free carpals, the cuneiform (cu) and the scapholunar (sc), are incompletely preserved. Compression of the specimen has caused a combined crushing and plastic deformation; where several bones were originally situated one on top of the other, their individual surfaces and limitations may now be difficult to trace in the fossil. This is evident in the wrist. The cuneiform *in situ* in the living bird is a U-shaped bone that



Figure 5. Pelvis of the holotype of *Plumumida lutetialis*. ?c.v., ?caudal vertebrae; d.p., dorsal parapophyses; f.h., head of right femur; fi., left fibula; l.f., left femur; l.il., left ilium; l.ti., left tibiotarsus; m., replica structure representing posterior synsacral vertebrae; p. 1–3, lumbar parapophyses; r.il., right ilium; r.is., right ischium; r.pu., right pubis; 3.s., bases of third pair of single parapophyses in the caudal section of the synsacrum; s.c., xiphial part of sternum with broken base of sternal carina; s.p., sternal plate; sy.v., anterior synsacral vertebra; t.v., thoracic vertebra; v.p., ventral parapophyses; y., posterior iliac crest; z., interior pelvic ridge.

embraces part of the carpal trochlea, with one branch lying on the underside of the wing. This branch can be seen in the fossil, a little distal to its original position because of a 90 degree turning over of the bone. The other branch, beneath part of the carpal trochlea, supposedly together with the external condyle of the ulna, has been pressed into the trochlear bone material, causing a swelling proximal to the visible branch of the cuneiform. The deformed trochlear bone mate-

rial is difficult to delimit from the fractured part of the cuneiform bone. Where unfragmented, the cuneiform shows a bulky shape with a median furrow, clearly visible in Figure 4, where may have lodged, judging from conditions in *Haematopus ostralegus*, the tendon that passes along the length of metacarpal II and fastens at the medial edge of digit II, together with (or forming part of) the exterior indicus longus tendon.

The carpometacarpus (cm), although easily identifiable in

the fossil, is not too well preserved with respect to details. The trochlear section, as stated above, has suffered a good deal of deformation; the terminal parts of ridges and processes are lacking, as can be observed in the trochlear ridge, the process of metacarpal I, the pisiform process (p.p) and the process pertaining to the pollical facet (p.f). The shaft of metacarpal II is fractured, with part of the bone wall lacking or covered by plast matrix. The proximal part of the shaft of metacarpal III is in replica. And, in the distal end of the carpometacarpus, part of the bone wall is lost, and the tuberosity of metacarpal II is either lost or, as it appears, is covered by plast. The distal metacarpal symphysis is fairly long, surpassing in length that in some Recent shorebirds, including *Haematopus ostralegus* and *Charadrius hiaticula*. *Scolopax rusticola* has a similarly long distal metacarpal symphysis that might indicate that this condition is a specialized character within the shorebirds. In doves the distal metacarpal symphysis is short.

Digit I (d.I), the pollex, is recognizable in the fossil, but is incomplete. It has not been possible to free its distal end (if preserved) from the resin.

Both phalanges of the second digit (d.II) are relatively well preserved. The proximal phalanx, as mentioned earlier, is of some diagnostic importance within the Charadriiformes. The medial part of the bone is strong and forms the axis of the element, with strong and elaborate metacarpal and digital facets. The lateral part consists of a thinner lamellar section, laterally bordered by a thicker edge or rim. In the fossil, the proximal lateral part of the bone is lacking. Distally, the lateral bone section terminates in the internus indicis process (p) that in the living bird was connected by ligamental tissue to the distal end of the second phalanx, thus, together with the latter, forming a good support for the base of the distal remex. The chevron-formed mark close to the interphalangeal joint was the base for a strong tendon to the proximal edge of phalanx 2. This bone in the fossil is partly covered by resin and cannot be seen in its full extent. Remiges were also fastened to the upper side of phalanx 1 (and to the first finger, carpometacarpus, and ulna). Its elaborated and strong articular ends, well developed tendon mark, and entire morphology, reminiscent of that in shorebirds, together with the morphology of the other preserved bones of the wing and shoulder girdle, indicate that *Plumumida lutetialis* was a capable flyer.

A "stray" bone fragment occupies the original position of the third finger.

The Pelvic Girdle. A good deal of the pelvis (Fig. 5), including the synsacral (sy.v—m) and post-acetabular right portions (r.il, r.is, r.pu), is comparatively well preserved.

In the synsacrum, the sacral section is covered by part of the shaft of the left femur (l.f). A structure regarded to be the broken base of the posterior right parapophysis (p.1) of the lumbar section can be identified anterior to it (above it in the figure), together with the bases of the second-to-last (p.2) and third-to-last (p.3) right lumbar parapophyses. The bone wall of the right side of the corresponding part of the synsacral body is preserved, although fragmented, whereas most of the wall in the left side is in replica. The structure marked "sy.v" is considered to be the anterior synsacral vertebral element (or it may be the posterior free thoracic vertebra). In spite of fragmentation, its posterior limitation can be perceived; modern birds may also have a terminal marking of the first synsacral vertebra. Between this and the three lumbar synsacral ele-

ments, represented by their right parapophyses, are the remains of still another element. Thus interpreted, the number of presacral vertebrae included in the synsacrum is five. A fairly well preserved vertebral body (t.v) is closely attached to the anterior end of the structure marked "sy.v," but not fused with it as is seen from its position a little out of line with the synsacral axis, and from the presence of terminal bone walls in the intervertebral joint area. It has preserved a large right anterior projection for the support of the rib.

The pelvis in birds exhibits some individual variation in morphologic details (see also Boas 1933). Thus the number of synsacral thoracic vertebrae may vary within a species. One available pelvis of *Haematopus ostralegus* has five fused presacral vertebral elements, whereas another pelvis of the same species has four fused presacral elements and one vertebra whose body is not fused with the synsacrum, but whose transverse processes and ribs support the anterior parts of the ilia. The vertebral body structure marked "sy.v" in Figure 5 may not have been completely fused with the axial structures behind it, but its position suggests that it was part of the pelvis. Fragments of lamellar bone (s.p) situated along the right side of the axial structure in the fossil are most probably parts of the sternal plate and do not belong to the ilium, thus giving no indication of the anterior extension of the pelvis. The morphology of the presacral part of the synsacrum, as far as it can be observed, is reminiscent of that in shorebirds, although the elements are more robust in the fossil than in shorebirds. As stated for *Haematopus ostralegus*, the synsacrum in modern shorebirds may include five presacral vertebral elements. In some shorebirds, such as *Vanellus vanellus* and *Calidris alpina*, the number is generally four. The corresponding part of the synsacrum in doves is shorter and more compact than that in shorebirds, with only three, or in some cases four, included vertebrae.

Posterior to the superimposed left femur is the caudal section of the synsacrum (*sensu* Howard 1929). Anteriorly, in the fossil's right side, remains of two pairs of dorsal (d.p) and ventral (right v.p) parapophyses, and in the left side, the undisturbed proximal parts of two ventral parapophyses (left v.p), can be distinguished. The presence of both dorsal and ventral parapophyses shows that the corresponding two vertebral elements are the first and second synsacral caudal vertebrae. The number of ventral parapophyses in this region in birds is also subject to some intraspecific variation, so that, e.g., some members of a species that generally has only one pair of ventral parapophyses may have two pairs, or one pair and a right or left ventral parapophysis in front or behind it. The two pairs of ventral parapophyses in the fossil were strong structures, which indicates that they represent a normal condition of two pairs for this species. Fragmented remains of their distal ends in the right side show that the two ventral parapophyses of each side converged distally, where, as known from Recent birds, they joined the inside of the ilium, thus forming struts from the synsacral body to the acetabular region. The ventral wall of the anterior part of the caudal section of the synsacral body is broad and flat. It is only slightly disturbed in the fossil and thus gives a fairly correct idea of the morphology of that part in the living bird also. Posteriorly, remains of three pairs of "single" (i.e., not "split into" dorsal and ventral) parapophyses can be seen. No synsacral bone material was preserved posterior to the third pair of single parapophyses (3.s),

and an indistinct replica contour (m) gives no morphologic details of the skeletal structure. But, judging from the shape of the neighboring part of the right ilium, which in the living bird was attached to the synsacrum, hardly more than one posterior vertebral element is lacking in the synsacrum. This would make six the number of caudal vertebrae included in the synsacrum. Fragmented bone walls remain in the two hindmost preserved interparapophyseal spaces (right side in the fossil), showing that these spaces in all probability were closed or nearly closed in the living bird. This also seems to have been the case in the most anteriorly preserved interparapophyseal space (between the double parapophyses). Matrix fills out the "background" in the intervening space, but lamellar bone fragments in the left side may also indicate the original presence of a bone wall in this interparapophyseal space. A structure in the fossil (?c.v), discernible in Figure 5 below and to the left of the caudal section of the synsacrum, is presumed to be the remains of the caudal vertebrae.

Most modern shorebirds have one pair of strong synsacral struts in the acetabular region of the pelvis, although two pairs of struts may occur. Doves have one, rarely two, pair(s) of comparatively weak synsacral struts. The number of synsacral vertebral elements posterior to the struts is generally four to five in shorebirds and five to six in doves. The interparapophyseal bone walls are usually fenestrated in the shorebirds, whereas in doves they tend to be closed.

The ilium, ischium, and pubis of each side are fused in *Plumumida lutetialis*, as are the corresponding bones in Recent birds. This leaves an ilio-ischiatic fenestra and a posterior incisure between the ilium and ischium, and an ischio-pubic fenestra or incisure between the ischium and pubis. Only fragments of the ilium (l.il) occur in the left side of the fossil. In the right side, because of compression, there is a large opening between the posterior part of the ilium and the synsacrum, which in many birds, including the shorebirds and (all?) doves, are not completely fused. The ilio-ischiatic fenestra has been closed by the ischium being pressed onto the lateral edge of the ilium (the presence of plast matrix obscures the details here). Most of the bone wall of the postacetabular part of the ilium is preserved (although fragmented), including a large posterior iliac process that in the present flattened condition exhibits transverse ripples, testifying to a certain degree of introflexion of the process in the living bird. The acetabulum has been protruded by the right femoral head (f.h), and the proximal parts of the right femur and of the left tibiotarsus (l.ti) and fibula (fi) have been pressed into the pelvic bone in the acetabular region causing fragmentation. The iliac bone wall between the distal ends of the right synsacral struts and the acetabulum is much disturbed and gives no information as to the original position of the struts relative to the acetabulum (see Strauch 1978:315). The interior pelvic ridge (z) has also been damaged in the acetabular region. The postacetabular part of this ridge, as far as it is preserved, is a strong and conspicuous structure in the fossil. It is almost straight, and continues posteriorly, where it is now broken, into the posterior ischial process. A bone structure beneath the posterior ridge fracture in the fossil may be the displaced fractured end of this process. Remains of a posterior iliac crest (y), which is the posterior limitation of the renal depression, can be observed connecting with the medial wall of the interior pelvic ridge. Along the lateral side of this latter structure is a fairly

large lamellar bone wall of the ischium, somewhat disturbed by the xiphial part of the sternum (s.c). The preserved section of the right pubis (r.pu) indicates by its strength that the pubes were well developed, and apparently extended a good distance behind the medial part of the pelvis.

In many pelvic features *Plumumida lutetialis* shows good correspondence with conditions in doves. The innominate bone, as far as it can be studied, is close in morphology to that bone in, e.g., *Columba loricata*. The synsacrum, by its broad ventral wall of the anterior caudal section and apparently closed interparapophyseal walls, is reminiscent of the synsacrum in, e.g., *Columba palumbus*. The presence of two pairs of strong synsacral struts in the acetabular region is, however, atypical of doves. In some modern columbiforms the pair of main synsacral struts extends from the vertebral element anterior to that corresponding to the main strut element in shorebirds. Following Strauch (1978:314), the condition in these doves is the relatively derived of the two. He states (ibid.) that, in the most widely distributed and presumably primitive state for the Charadriiformes, the pair of main struts arises from the fifth vertebra from the posterior end of the synsacrum. The interpretation given above of the number of caudal synsacral elements in the fossil would permit the conclusion that the two pairs of synsacral struts in *Plumumida lutetialis* correspond to a combination of those of the shorebirds and those of the advanced doves. Thus, in this particular feature, *Plumumida lutetialis* may represent a form intermediate between shorebirds and advanced doves. Another interpretation is that both pairs of struts that may occur in specimens of modern shorebirds were strongly developed in *Plumumida lutetialis* as a consequence of the general robustness of the pelvis, which might also be said for other features that give the impression of strength. Recent shorebirds may have more than four, and doves more than five, caudal synsacral elements posterior to the strut element, suggesting that the number of caudal vertebrae included in the synsacrum is of limited diagnostic significance. Unfortunately, the sacral section, which would permit a correct determination of the homology of the vertebral elements in this region, is covered in the holotype.

The Hindlimbs. The greater portions of both hindlimbs (Figs. 5 and 6) are visible in the fossil, but their state of preservation permits few fine details to be studied. The right hindlimb (Fig. 6) is positioned in articulation with the pelvis, with the femoral head (f.h) located in the acetabulum as described above. Sections of the right femur (r.f) are seen as bone fragments or impressions in the matrix to the left of the superimposed left tibiotarsus (l.ti). The distal condylar part of the femur is crushed into more or less complete fusion with the crushed proximal articular part of the right tibiotarsus (r.ti). The femur length of 36 mm is measured between the visible extremes of the femur in the fossil, indicated in Figure 6 as the end points of the white lines "r.f." The original femur may have been slightly longer. In the proximal part of the right tibiotarsus, which is seen in anterior view, a distinct mark for the attachment of the M. flexor cruris medialis (f.a) can be observed. A ridge (on various fragments of bone), the intermuscular line (i.m), terminates proximally in the base of the (broken) inner cnemial crest (c.c). Because of the serious crushing of the proximal end of the tibiotarsus, the proximal continuation of the inner cnemial crest cannot be reliably indicated. A replica con-

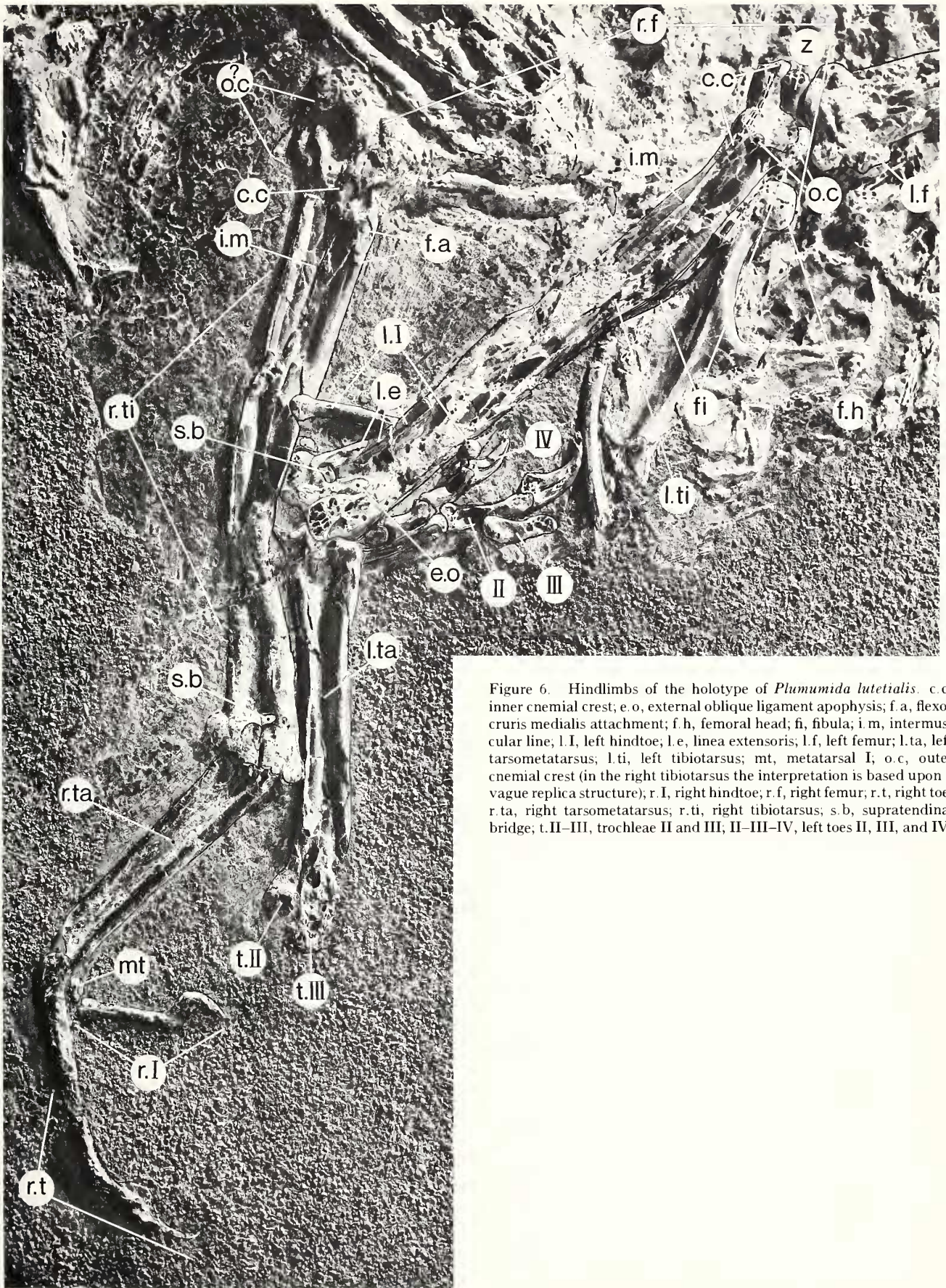


Figure 6. Hindlimbs of the holotype of *Phumumida lutetialis*. c.c, inner cnemial crest; e.o, external oblique ligament apophysis; f.a, flexor cruris medialis attachment; f.h, femoral head; fi, fibula; i.m, intermuscular line; l.I, left hindtoe; l.e, linea extensoris; l.f, left femur; l.ta, left tarsometatarsus; l.ti, left tibiotarsus; mt, metatarsal I; o.c, outer cnemial crest (in the right tibiotarsus the interpretation is based upon a vague replica structure); r.I, right hindtoe; r.f, right femur; r.t, right toe; r.ta, right tarsometatarsus; r.ti, right tibiotarsus; s.b, supratendinal bridge; t.II–III, trochleae II and III; II–III–IV, left toes II, III, and IV.

tour is tentatively interpreted as the imprint of the outer cnemial crest (?o.c). The shaft of the right tibiotarsus has undergone a special fragmentation because of lateral pressure from bones of the left hindlimb, resulting in a slight bending and some extension in a zone close to the present location of the proximal end of the left tarsometatarsus (l.ta), where little bone material is preserved. Part of the original bone wall remains near the distal end of the tibiotarsus, but around the intertarsal joint, most morphological details are obscured by intense crushing of the opposing ends of the tibiotarsus and the tarsometatarsus. One bone structure, the supratendinal bridge (s.b), appears strangely unaffected by the crushing. Rounded structures (set off in the figure) apparently represent the condyles. No trace of a right fibula can be seen. The remains of the right tarsometatarsus (r.ta) show an element with a wide median furrow. Some bone material is preserved, but most of the element appears in replica. Distally, the trochleae have not been preserved. Their termination was originally located a little distal to the base of the hallux (r.I). A fracture now occurs in the tarsometatarsus above the hallux articulation. The hallux, also in replica, has been determined on the basis of the presence of a small body (mt) interpreted as metatarsal I, and on the structure of the toe that seems to consist of one larger element and a curved and pointed distal segment, corresponding to the first and the ungual phalanges, respectively. The terminal structure (r.t), ending in a "claw," is also a toe replica, but the number of the toe cannot be determined since no reliable traces of articulation can be discerned.

In the left hindlimb (Figs. 5 and 6), the femur (l.f) is incompletely preserved, with the proximal part lacking, and the bone wall in the remaining part strongly fragmented. The left tibiotarsus (l.ti) is seen in its full length. Proximally, the base of the inner cnemial crest (c.c) can be traced, together with parts of the bone wall, medial and lateral to the crest. A broken structure (o.c) represents the outer cnemial crest. The bases of these two crests extend about similar lengths distad in the tibiotarsus. An intermuscular line (i.m) can be followed as a distal continuation of the inner cnemial crest for some length of the bone. The middle part of the shaft is much fragmented, with pieces of the bone wall lacking. Towards the distal end of the bone, a very clear linea extensoris (l.e) can be traced in three fragments, terminating distally in the broken internal oblique ligament apophysis. The external oblique ligament apophysis (e.o) is preserved in the fossil, as well as the supratendinal bridge (s.b). The distal condyles, although incomplete, are recognizable, as is the condylar fossa between them. Both condyles have suffered some deformation because of pressure against the surrounding bones. Sections of the fibula (fi) are preserved in what appears to be the complete original extension of the bone. Its proximal "head" is rather large.

The left tarsometatarsus (l.ta), in its exposed anterior side, has much bone material preserved. Proximally, the external cotyla has become somewhat deformed by the external condyle of the tibiotarsus being pressed into it. The internal cotyla is little disturbed. The depth and length of the anterior median furrow was artificially increased during the fragmentation of the bone by the left lateral wall being turned into the furrow. There was probably a median furrow in the upper part of the undisturbed tarsometatarsus, perhaps as wide as that seen in the remains of the right tarsometatarsus. But in the distal end of the bone, metatarsal III protrudes, thus making the front

side of the bone convex. The remains of trochlea II (t.II) and trochlea III (t.III) show that the latter was the distalmost of the two, and presumably of all three trochleae. Trochlea IV is not preserved. No digits are found in natural articulation with the left tarsometatarsus, but partially articulated toe bones located around the distal end of the left tibiotarsus are considered to belong to the left foot. A long bone (left portion of l.I), situated transversely between the right and left tibiotarsi, is believed to be the proximal phalanx of the left hallux, corresponding in size to that in the right hallux (r.I). Its ungual phalanx may be the one exposing its hemispheric flexor tubercle (l.I), with a central foramen, close to the lateral side of the left tibiotarsus and pointing its distal tip along this bone in its proximal direction. Below it are two articulated toe structures that show strong, curved, and pointed ungual phalanges with transversely rounded undersides and deep lateral furrows. Four phalanges, of which the two middle ones are comparatively short, can be seen in one, and, in the other, two phalanges and the ungual phalanx are visible. In birds, four bones may occur in toes III and IV, and three bones may also occur in toe II. The interpretation of the two articulated toes shown in Figure 6 as toes II and IV, and the free phalanx representing toe III (or with numbers II and III interchanged) would correspond to conditions in, among others, doves.

No morphologic peculiarities of diagnostic interest can be studied in the fossil femora. The tibiae exhibit features that show similarity to the shorebirds and, for some of them, distinguish the fossil from the doves. In shorebirds, the M. flexor cruris medialis attachment is primarily a distinct oblong marking situated on the bone as it is in the fossil, whereas in doves the marking is different in shape, and is often more diffuse in outline than in shorebirds. Some shorebirds, such as *Vanellus vanellus* and *Calidris alpina*, have the bases of the inner and outer cnemial crests about equally long; this may, however, also be the case in some doves. The internal oblique ligament apophysis is in *Plumumida lutetialis* and Recent shorebirds situated rather closely above the level of the supratendinal bridge; in doves it is located farther proximad on the shaft of the bone. It appears in the fossil that the external condyle of the tibiotarsus is larger than the internal condyle; such is the case in shorebirds, but not in doves, where the internal condyle tends to be the larger.

The foot in *Plumumida lutetialis* is reminiscent of the foot in doves. Characters encountered in a moderately advanced perching foot include a relatively short and strong tarsometatarsus, and robust digits consisting of a long hallux and, as it also appears, three anterior toes of medium lengths, all with strong, curved, and pointed (although not to the extent seen in passeriforms or birds of prey) claws. Specialized perchers, as the Passeriformes, have all three trochleae of the tarsometatarsus in one line, whereas groundbirds, as the Charadrii, have trochlea III longer and more anteriorly protruding than trochleae II and IV (compare Stegmann 1969:25 ff). The dove foot seems intermediate in morphology and evolutionary stage between that in groundbirds of the shorebird type and the advanced perching foot.

The tarsometatarsus in Recent doves has no well developed anterior median furrow as has the tarsometatarsus in Recent shorebirds and, apparently, in *Plumumida lutetialis*. In doves the tarsometatarsus is shorter than the femur, whereas in shorebirds it is longer, in some cases much longer, than the

femur. In *Plumumida lutetialis* the two bones are of about equal length. As stated above, Recent shorebirds exhibit various degrees of reduction of the hallux, showing that the plesiomorphic state in this group of birds is the presence of a hallux. In skeletal morphology and proportions the foot of *Plumumida lutetialis* appears to be intermediate between that of shorebirds and doves.

CONCLUSIONS

There seems to be fairly wide agreement that the Columbiformes developed from early Charadriiformes, perhaps during late Cretaceous times (for various elaborations of the idea, see cited works by Fjelds  and Stegmann, and works referred to therein). It is tempting, on the basis of the above description, to see in *Plumumida lutetialis* a form "on the line" from early shorebirds to doves. Only one pre-Lutetian columbiform, *Microena goodwini* Harrison and Walker 1977, described from the British Lower Eocene on the basis of a left tarsometatarsus lacking the trochlea for the 4th digit, has been recorded. Shorebirds are known as far back as the late Cretaceous (see Brodkorb 1967 and later works such as Brunet 1970 and Harrison and Walker 1976, 1977). *Rhynchaetes messelensis*, stated by Wittich (1898:144) to be intermediate between shorebirds and rails, is referred to the Scolopacidae by Brodkorb (1967) (on the basis of Wittich's investigations), an allocation that is, however, questioned by some workers.

Most features in the fossil specimen used to refer it to the shorebirds are believed to be plesiomorphic characters within the shorebird complex (i.e., the shorebirds and groups derived from them). A perching foot is a relatively apomorphic character therein.

Perching birds are found in various taxa of typically non-perching groups, such as the Cairinini within the Anseriformes, and *Anous* spp. within the Lari. In both the perching ducks and geese and the noddies, the hindtoe is markedly long and the claws are more robust than in other ducks and terns. The whole foot, however, is not very different from the foot in their close relatives. Yet it is said about the young of these birds that they have very strong claws and are good at climbing. Very advanced perching feet are encountered in the Passeriformes, less advanced in the Columbiformes. A perching foot with corresponding structural modifications in the hindlimb and pelvic girdle is a specialization that evidently developed more than once in bird history.

One feature in the fossil, the short glenoid lip-long glenoid facet structure in the coracoid, does not have a morphologic parallel in the investigated shorebirds and doves. Although encountered in other bird taxa, it seems to be unique for *Plumumida lutetialis* among known shorebirds and doves. The character is considered an autapomorphy for the taxon to which the fossil belongs.

The long distal metacarpal symphysis distinguishes *Plumumida* both from doves and from those shorebirds that are generally regarded as unspecialized. Specialized shorebirds, such as *Scolopax*, also have a long symphysis of the distal ends of metacarpals II and III. The character, presumably, is relatively apomorphic within the shorebirds, but is encountered within other bird taxa also.

Formally, following the above given statements, *Plumumida lutetialis* should be placed within the shorebird-complex

as a separate taxon (because of autapomorphy) with sister-group status relative to either (1) the doves (synapomorphy: the perching foot), or (2) the *Scolopax* group (synapomorphy: the long distal metacarpal symphysis). For the present, however, acknowledging the incompleteness of the fossil, *Plumumida lutetialis* will be placed *incertae sedis* in the Charadrii.

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